

SOME WESTERN COLUMBINES

BY T. D. A. COCKERELL

Last year (Contrib. U. S. Nat. Herbarium, 20: Part 4) Mr. E. B. Payson published a most interesting revision of the genus *Aquilegia* as found in North America, and this will naturally serve as a point of departure for new investigations. The subject is a difficult one, owing to the fact (as it seems to be) that any species in the genus will freely cross with any other; and, at least in our experience, the hybrids themselves are perfectly fertile. Thus, on grounds similar to those which convince us that there is only one living species of *Homo*, it may be maintained that there is possibly only one genuine species of *Aquilegia*. Nor is this all; just as *Bursa bursa-pastoris* var. *heegeri* (commonly called *Bursa heegeri*) is a form lacking the most prominent character of the genus to which it belongs,* so *Aquilegia vulgaris* var. *stellata* and *A. caerulea* var. *daileyae* lack the generic character of spurred petals, so that but for their obvious general affinities we might not regard them as columbines at all. This plasticity is remarkable in a genus which in many respects seems highly modified. The long spurs are adapted to the visits of butterflies, but I have seen a bumble-bee (*Bombus*) slit up a spur from the side, and thus get at the nectar illegitimately. The columbine in which this occurred was *A. caerulea*. Mr. Payson suggests that "the modern species of *Aquilegia* seem to have been developed from species having blue flowers. These seem first to have given rise to white-flowered, these to yellow-flowered, and these finally to red-flowered species." There is apparently no basis for such an evolutionary sequence, for the yellow in the flowers is due to plastids, readily visible under the microscope; while the blue and red are equally due to anthocyanins, held in solution in the sap. Gaston Bonnier, in his scheme of relationships of Ranunculaceous genera, indicates an affinity between *Aquilegia* and *Helleborus*, while the latter leads back to *Caltha*, etc. The suggestion might be, that the original columbines were

* For a good figure, see Shull, Zeits. f. indukt. Abstamm. u. Vererbungslehre. 12: 98. 1914.

yellow or white, if there was any well marked sequence in the evolution of color. Purple, however, is already a prominent color in species of *Helleborus*, and it is evident that anthocyanins and yellow plastids both antedate the evolution of *Aquilegia*.

A few years ago* I described a hybrid between *A. desertorum* and *A. chrysantha*. Our plant of *A. desertorum*, obtained in Santa Fé Cañon in 1912, and then evidently of considerable age, is as vigorous as ever in 1919. It proves fertile with its own pollen, and we have seedlings from it already in flower, perfectly true to type. It has been and still is a question whether the differences between *A. desertorum* and *A. elegantula* may be due to environment and hence not truly specific. Mr. Payson treats them as distinct species, but declares that *desertorum* is known only from Arizona, though he quotes my remarks on the New Mexico plant. A specimen obtained by Heller nine miles east of Santa Fé, and therefore very near the locality of my *desertorum* plant, is referred by Payson to *elegantula*. An analysis of the characters of my plant, with Payson's descriptions before me, appears to indicate *desertorum* rather than *elegantula*, but it agrees perfectly with neither. The leaves are early glaucous, but at maturity clear green above. Only the leaflets of the flowering stems are small; the basal leaves have them very large, the apical leaflet 40 mm. long and 38 wide. The better developed flowering stems bear well-developed leaves, but this can hardly be a specific character. The leaflets have a quite dense erect pubescence on the under side, which is a *desertorum* character. (*A. chrysantha* has this pubescence less dense, but still very evident; but singularly enough the *chrysantha* × *desertorum* hybrid has only a very few widely scattered hairs.) The spurs are about 22 mm. long, thus agreeing better with *desertorum*, and the sepals are red, pallid at tip. The original *elegantula*, as described by Greene, had light green sepals. The sepals however are erect, not spreading as they should be in *desertorum*. The follicles have the tips widely spreading.

On the basis of the above characters, it might appear that the Santa Fé Cañon *desertorum* should be separated both from the

* Botanical Gazette 62: 413. 1916.

true *desertorum* of Arizona and the typical *elegantula* from near Mancos, Colorado. It seems more probable, however, that all three represent phases of a single species. Mr. D. M. Andrews has recently collected *elegantula* in Colorado, and thinks that it is separable from my plant on account of the habit of growth. We do not yet know how far this may be due to differences in environment.

The F₂ plants from *desertorum* × *chrysantha*, raised by my wife, flowered this year. The most curious form shows doubling, with twisting of the spurs. The spurs vary from 6 to 9, but the laminae of the petals are supplemented internally by a variable number of emarginate laminiform appendages.

This year we have an authentic *A. caerulea* × *desertorum* in flower. The flowers are formed as in *caerulea*, with pure white laminae; but are smaller, the sepals pale lilac tipped with white, the spurs rosy-lilac. In bud the spurs are suffused with red. The leaflets are pubescent beneath, the hair short but abundant. Spurs 28 mm. long, laminae 11 mm; sepals about 20 mm. long and a little over 8 mm. wide. In full flower the spurs are moderately divergent. The leaflets are large, even on the flowering stems.

We also have this year a varied series of F₂ plants from *A. caerulea* × *chrysantha*. *A. chrysantha* has yellow flowers, often with some anthocyan tints, which then are red, but never sufficiently to affect the general yellow effect. The sepals are pre-vaillingly narrower than in *caerulea*, but variable. The F₁ from *caerulea* × *chrysantha* is pale blue with the laminae yellow, fading to nearly white. The F₂ plants include such as the following:

(a) Form of *caerulea*, with broad sepals, but laminae entirely bright lemon yellow; sepals dilute rosy purplish, more or less suffused with yellow, especially at tips; spurs pale yellow, apically suffused with dilute purplish; buds strongly pinkish, including spurs. Thus the buds show the acid state of the anthocyanin, which is retained to maturity in *chrysantha*, but the hybrid is affected by the *caerulea* ancestry. This type of F₂ hybrid occurs only in a small percentage of the plants.

(b) Sepals broad as in *caerulea*; flowers white, very delicately tinted with purple on sepals and often on spurs.

(c) Similar to the above, but with less of the purplish tint (more on spurs), and the whole flower (especially laminae) is very pale yellow. Others show more of the purplish and brighter yellow, intermediate between a and c.

The factorial analysis of these forms cannot yet be clearly made. *A. caerulea* in the western part of its range is not blue but white, but there is no evidence that the plants we used carried a recessive white. We can however postulate that yellow plastids (*chrysantha*) are allelomorphic to their absence (*caerulea*), and abundant anthocyanin (*caerulea*) to little or none (*chrysantha*). If we call the factors respectively P, p, A, a, the F₁ hybrid will have the formula PpAa, and will combine blue with yellow, as it actually does, with non-acidity also dominant over the acid condition of *chrysantha*. In the F₂ 9 out of 16 should look like the F₁; three should resemble *caerulea*, three *chrysantha*, and one might be expected to be white, feebly or not tinted with anthocyanin. Evidently other factors are involved, for as a matter of fact the pallid (supposedly double recessive) flowers are numerous.

Genuine *A. caerulea* produces some hitherto unrecorded variations. Mr. D. M. Andrews has at Boulder, Colorado, a large stand of very fine and typical *caerulea*, the seed having been obtained from the Blanchard ranch in Boulder Cañon. The strain originated in the nearby mountains, and is in general extremely uniform. But as Mr. Andrews pointed out to me, there are a few plants abruptly and conspicuously varying from the type:

1. Laminae of petals blue like the sepals, elongate, narrow (e.g., 40 mm. long and 8 wide); spurs normal, varying to small and more or less aborted. A few plants. This is more or less intermediate between the typical form and variety *daileyae*, but distinct from both.

2. Flowers very pale, light yellowish or greenish in bud, eventually delicately tinted with purplish. Sepals and petals 9 to 10, the sepals reflected at maturity, placed just below the outwardly-turned spurs; laminae remaining erect, lanceolate, about as long (20 mm.) as the spurs. The sepals are mainly

pale green, the laminae delicate purplish one plant only. This has an atavistic appearance, and is quite without the beauty of normal *caerulea*.

These observations indicate that *Aquilegia* is an unusually favorable genus for the investigation of genetic problems. Some of its advantages are the following: (1) The ready hybridization and fertility of the F_1 ; (2) the tendency to mutate, apart from crossing; (3) the existence of spurred and spurless forms, and of forms with and without colored plastids and anthocyanin colors; (4) the heterozygotes can be easily preserved and propagated by dividing the crowns; (5) incidentally, beautiful and interesting garden plants are produced.

SHORTER NOTES

Rhamnus dahurica IN MICHIGAN.—South of Ann Arbor, Michigan, is an extensive area of level ground formerly occupied chiefly by tamarack, black ash, and other hydrophytic trees. The ground water lies always near the surface and parts of the area were originally very swampy. Recent construction of drainage systems has destroyed much of the swamp, which has been put under cultivation, but the rest of the tract is still in forest.

Five years ago a forestry class of the University of Michigan discovered in the heart of the swamp a tree unknown to them. It was submitted to the writer for identification and proved to be *Rhamnus dahurica*. It was then supposed that the tree had been planted by Mr. J. B. Steere, who owns part of the land and had travelled extensively in the Orient. In 1916 Mr. Steere pointed out a second tree to the writer, some two miles from the first one, with a request for its identification. He was surprised to learn its name and disclaimed any knowledge of its origin. Only one tree of the species is known in cultivation in the vicinity, which, since it is a smaller tree, can scarcely be considered as the parent of these two individuals.

The two apparently wild trees are 500 yards or more from any residence, either past or present. One is in the middle of a forest